DOCUMENT RESUME

ED 349 158 SE 052 405

AUTHOR Kindfield, Ann C. H.
TITLE Biology Diagrams: Tools To Think With.
PUB DATE Apr 91
NOTE 52p.; Paper presented at the Annual Meeting of the American Educational Research Association (Chicago, IL, April 1991).
PUB TYPE Reports - Research/Technical (143) -- Speeches/Conference Papers (150)

EDRS PRICE MF01/PC03 Plus Postage.
DESCRIPTORS Biology; Diagrams; Educational Research; *Genetics; Higher Education; *Problem Solving; *Protocol Analysis; *Qualitative Research; Science Education; Science Instruction; Thinking Skills
IDENTIFIERS Chromosomes; *Expert Novice Problem Solving; *Microanalysis

ABSTRACT

Subcellular processes like meiosis are frequently problematic for learners because they are complex and, except for the extent that they can be observed under a light microscope, occur outside of our direct experience. More detailed characterization of what underlies various degrees of student understanding of a process is required to more fully inform the design of useful instruction. This qualitative study used microanalytic techniques to characterize expert/novice reasoning on meiosis, with the primary focus on the role played by domain-specific diagrams. Three groups, labelled the expert group, experienced novices, and inexperienced novices, were created based on their expertise in genetics and were each composed of five subjects. Subjects were asked to think aloud as they solved genetics problems. Follow up questions were used to have the participants elaborate on the biological concepts mentioned and diagrams drawn. Results indicate that experts create chromosome diagrams that are more fine-tuned to the relevant biology and use them to: (1) support internal thought processes; (2) record information; (3) check preceding reasoning; and (4) illustrate components of their problem solutions. Based on the research, the paper recommends that instruction concerning expert pictorial skills and reasoning should be incorporated into meiosis instruction. Students should be assessed for both verbal and pictorial knowledge/reasoning. The appendixes include a review of meiosis and chromosome diagrams. (Contains 15 references.) (PR)

****
* Reproductions supplied by EDRS are the best that can be made *
* from the original document. *
****

"PERMISSION TO REPRODUCE THIS MATERIAL HAS BEEN GRANTED BY
Ann C.H. Kindfield

TO THE EDUCATIONAL RESOURCES INFORMATION CENTER (ERIC)."

U.S. DEPARTMENT OF EDUCATION
Office of Educational Research and Improvement
EDUCATIONAL RESOURCES INFORMATION CENTER (ERIC)

☒ This document has been reproduced as received from the person or organization originating it.

☐ Minor changes have been made to improve reproduction quality.

• Points of view or opinions stated in this document do not necessarily represent official OERI position or policy.

ED349158

Biology Diagrams: Tools To Think With

Ann C. H. Kindfield
(formerly Ann C. Hildebrand)
McDonnell Postdoctoral Researcher
EMST
4533 Tolman Hall
UC Berkeley
Berkeley, CA 94720
annie86@violet.berkeley.edu

Paper presented at the Annual Meeting of the American Educational Research Association, Chicago, April 1991, as part of the symposium *Microanalysis and the Classroom Curriculum: Specific Lessons about Learning Problematic Concepts in Mathematics and Science.*

This work was funded in part by a dissertation year fellowship from the Spencer Foundation and a postdoctoral fellowship from the James S. McDonnell Foundation.

SE 052 405

BEST COPY AVAILABLE

Introduction

In the domain of biology, particularly genetics, students are faced with the task of constructing working knowledge of subcellular processes like mitosis and meiosis. That doing so is often problematic has been well documented in a variety of studies of student conceptions and problem solving in genetics (Hackling & Lawrence, 1988; Hildebrand, 1985; Slack & Stewart, 1990; Smith, 1988, 1990; Stewart & Dale, 1989; Stewart, Hafner, & Dale, 1990). Subcellular processes are inherently complex and, except for the extent to which they can be observed under a light microscope, basically occur outside of our direct experience. These factors certainly contribute to the difficulties that students experience when learning about such processes. However, awareness of these general factors alone does not provide great insight into the nature of instructional interventions that might facilitate student understanding of specific pieces and types of process knowledge and address common student difficulties. More detailed characterization of what underlies various degrees of understanding of a process is required to more fully inform the design of useful instruction.

More detailed characterization of the components underlying individuals' understanding of a variety of topics can be gained through the microanalysis of their behavior while reasoning about a topic of interest. By microanalysis I mean the detailed qualitative analysis of individual or group behavior from which generalizations about components of reasoning and underlying understandings can be derived. These generalizations can then serve to inform both models of reasoning, understanding, and learning and the design of instruction which can be further tested for validity and efficacy.

Specifically with regard to subcellular biological processes, I utilized microanalytic techniques to characterize expert/novice reasoning about one key process, meiosis (Hildebrand, 1989). The primary focus of this study was on the role

played by domain-specific diagrams in reasoning about and understanding meiosis. I chose meiosis because (1) it is the primary process of basic transmission genetics, a core component of the introductory biology curriculum and (2) characterization of meiosis knowledge and reasoning would complement and extend previous research on transmission genetics problem solving (see above references). I focused on diagrams because (1) diagrams of participating entities and process states are the common external form of scientific models of subcellular biological processes, (2) these common external forms are ubiquitous in biology instruction, and (3) specifically with regard to genetics, the multiplicity of instructional diagrams and the typical lack of instruction concerning how they are related to one another have been implicated as a source of student misconceptions and difficulties in this domain (Cho, Kahle, & Nordland, 1985).

Detailed microanalysis of individual reasoning generally revealed an intricate interconnection between individuals' knowledge of meiosis and the quality and uses of diagrams they generated when reasoning about the process. More specifically, the more expert participants in this study displayed a variety of systematic diagram-related reasoning behaviors that were absent among the novices. Further, these results suggest that in the development of understanding of meiosis, meiosis knowledge and pictorial skill (i.e., the behaviors/knowledge associated with the quality and uses of diagrams) coevolve. This pictorial skill, which appears to be a crucial component of a meaningful understanding of meiosis and is virtually never addressed in instruction, is the focus of this paper.

Methods

Five subjects from each of three levels of expertise in genetics participated in this research. The *expert* group consisted of one university professor, two visiting lecturers, and two advanced graduate students from the UC Berkeley Department of

Genetics (3 females/2 males). The *experienced novices* were five senior undergraduate genetics honor students at UCB who had already completed their core genetics courses (with A averages) and who were concurrently working in genetics research laboratories on senior thesis projects (2 females/3 males). The *inexperienced novices* were five UCB undergraduate biology majors concurrently enrolled in an introductory genetics course (3 females/2 males). The five inexperienced novices had all scored above 87% on their first midterm exam and were interviewed following classroom exposure to meiosis.

Participants completed a 1.5-2 hour individual interview during which each worked on a non-traditional genetics problem in a combined think-aloud/clinical interview setting, answered interviewer follow-up questions, and identified and discussed a series of standard diagrammatic representations of DNA, genes, and chromosomes. Some participants were asked to draw for purposes of clarification during follow-up questioning but no references to or requests for drawing occurred during the problem-solving portion of the interview.

The genetics problem, designed to require direct reasoning about the process of meiosis, consisted of a verbal description of a particular eukaryotic cell, three individually presented sets of gametes that could result from this cell going through meiosis (having increasingly complex solutions), and a request to describe the specific meiotic events that would lead to the formation of each gamete set. The cell description, request, and each gamete set were presented on individual 4 X 6 cards as shown in Figure 1.

Some interviewer follow-up questions were routinely asked during each interview, but most follow-up questions were tailored to individual's behavior while working on the problem. The general intent of these questions was to have participants elaborate on biological concepts they mentioned and diagrams they drew while problem solving. During follow-up questioning, the inexperienced

Card 1

Suppose you have a diploid cell from a eukaryotic organism for which the haploid chromosome number is 2 (N=2). The organism is heterozygous for three different genes -- a, b, and c. The a and b genes are genetically linked, while the c gene is located on a different chromosome.

Card 2

Suppose that you can directly observe the genotypes of the four gametes that result when a **single diploid cell** undergoes meiosis. With respect to genes a, b, and c, what events would have to occur during the **specific** meiosis that gives rise to each of the sets of gametes on the following cards?

(NOTE: Each set of gametes is the result of a single diploid cell undergoing a **single** meiosis; 1's and 2's indicate the parental origin of each of the alleles.)

Card 3

i) $a_1b_1c_2$ $a_1b_1c_2$ $a_2b_2c_1$ $a_2b_2c_1$

Card 4

ii) $a_1b_1c_1$ $a_1b_1c_2$ $a_2b_2c_1$ $a_2b_2c_2$

Card 5

iii) $a_1b_1c_2$ $a_1b_2c_1$ $a_2b_1c_2$ $a_2b_2c_1$

Cards 4 and 5 were presented only after an individual had completed her/his work on the preceding gamete set.

Figure 1. The cell description and problem presented to each participant. Cards refer to individual 4 X 6 on which various pieces of information were presented.

novices were also asked to diagrammatically represent the described cell going through meiosis.

After the completion of all problem solving and follow-up questioning, participants were sequentially shown the 10 standard representations in Figure 2, each of which was printed on a 4 X 6 card. After identifying and discussing individual representations, each participant was asked to compare eight specific pairs (5&9, 5&2, 5&7, 5&6, 6&7, 4&6, 3&4, 3&7), focusing on the correspondence between components and size relationships.

All interviews were videotaped and the audio portions were transcribed. Videotapes, transcripts, and participant-generated diagrams served as the data analyzed for this study. In order to perform detailed microanalysis of individuals' behavior, these data were treated as follows: Transcripts were subdivided into problem solving, follow-up questioning, and standard representations segments, and videotapes were reviewed in order to coordinate the text of the transcripts with the timing of and/or references made to subjects' drawings. Original drawings were numbered, and specific diagram numbers along with brief notes were inserted at appropriate points in the transcript. Next, fully annotated transcripts were created for each subject's work by first converting each transcript to a two-column format with text appearing in the left-hand column. Then, from detailed review of the videotapes, parenthetical notes describing subjects' observable behaviors were added to the text of each transcript. Notable behaviors included (1) diagram-generating activities like beginning, modifying, or completing a diagram, (2) diagram-utilizing activities like looking at or pointing to particular diagram(s) or diagram component(s), and (3) general problem-solving-related activities like re-reading the cell description or problem statement. These behaviors could occur while subjects were talking or while they were silent. When a behavior occurred during a period of silence, the length of the pause was added to the description. Pauses of 2 seconds

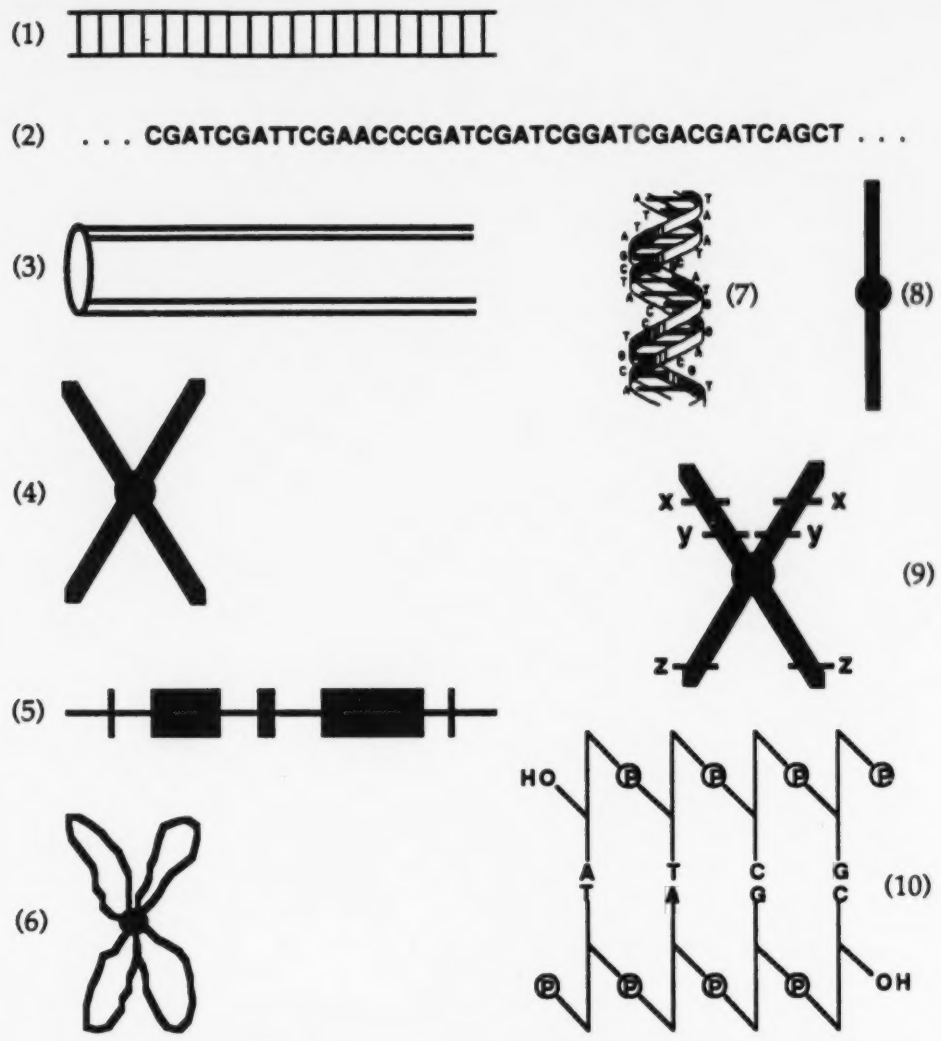


Figure 2. Standard representations (numbers adjacent to each representation indicate their order of presentation during the interview). (1) double-stranded DNA, (2) single-stranded DNA, (3) replicated chromosome, (4) replicated chromosome, (5) gene, (6) replicated chromosome, (7) DNA, (8) unreplicated chromosome, (9) replicated chromosome, (10) DNA.

or greater were considered significant enough to be noted. Finally, free-hand reproductions of subject diagrams associated with particular text segments were added to the right-hand column of annotated transcripts adjacent to the text with which they corresponded. Subjects' original diagrams collected at the end of each interview were obviously static, completed versions. If an original diagram was generated in the absence of interruption by some other activity, the reproduction consisted of the completed version of that diagram. However, if an original diagram was generated in a piecemeal fashion, the reproduction consisted of the series of partial diagrams (derived by observing individual pencil strokes on the videotape) that ultimately led to the completed version. In addition, when a previously completed diagram was later modified, the reproduction included both 'before' and 'after' versions of the diagram. (A sample annotated transcript is available upon request.)

Results

The results of interest in this paper are primarily those concerning the quality and uses of diagrams generated by the the more expert participants in the study. These participants displayed knowledge-dependent representational variability, that is, they fine-tuned their diagrams by adding or subtracting features as particular features were relevant to the immediate reasoning task. In addition, these participants systematically used their fine-tuned diagrams to support internal thought processes, record information, and check previous work while actively engaged in reasoning, as well as to illustrate their solutions at the completion of a problem. Because of the intricate interrelationship between knowledge of meiosis and expert diagram-related reasoning behaviors, it is difficult to describe these behaviors more fully in the absence of some knowledge of meiosis. Therefore, I first

provide a brief description of relevant meiosis knowledge followed by elaborations of experts' meiosis knowledge and diagram-related reasoning behaviors.

Basic Meiosis Knowledge

Meiosis is the process by which two sets of chromosomes present in one initial cell nucleus are ultimately distributed among four nuclei such that nuclei of each of the four product cells formed following cell division contains only one set of chromosomes. In females, the product cells are eggs or ova, and in males, the product cells are sperm (for animals) or pollen (for plants). Thus, the product cells of meiosis are the sex cells, pairs of which can fuse at fertilization initiating the production of offspring.[1]

In generic form, any process can be thought of as some object or objects undergoing a series of movements/interactions that result in some outcome. In the process of meiosis, chromosomes (the biological objects/entities consisting of DNA, the genetic material), go through a specific series of movements/interactions that result in the production of sex cells. Specific chromosome movements/interactions are constrained by certain aspects of the three-dimensional structure of these biological objects and the order in which the movements/interactions occur. At the beginning of meiosis, chromosomes are replicated and condensed such that under a light microscope, they have four visible, easily depictible structural features: dimensionality, shape, two identical subunits (sister chromatids), and a constriction where the two subunits are joined (the centromere). A series of typical

[1] Certain organisms do maintain haploid (i.e., one-set-of-chromosomes) nuclei following meiosis as one (possibly the primary) component of their life cycle. Beyond contributing specifically to the formation of sex cells, meiosis more generally functions in the production of genetic variability through the reshuffling of specific versions of genes (alleles), that is, it serves as one of the two primary components of a sexual reproductive cycle. This variability is further enhanced when two haploid cell nuclei fuse to form a diploid (containing two sets of chromosomes) nucleus, the other primary component of a sexual reproductive cycle. Thus, though not necessarily transient (as are human eggs and sperm), meiotic products or their descendents ultimately function in sexual reproduction.

representations of replicated chromosomes, ranging from one that explicitly depicts all four structural features to one that depicts none of these structural features is shown in Figure 3.

Of the four easily depictible chromosome structural features, only two, the presence of two subunits and the centromere, have a direct bearing on the specific outcome of a particular occurrence of meiosis. More specifically, these two features impact the outcome of crossing over, one of the series of chromosome interactions that occurs during meiosis.[2] Briefly, since a cell about to undergo meiosis contains two sets of chromosomes, each chromosome has a partner that consists of nearly identical DNA molecules and therefore the same linear array of genes (units of genetic information encoded in the DNA). Slightly different versions (alleles) of the same gene can exist so one of the partner chromosomes can contain, for example, the a_1 version of the a gene, and the other partner can contain the a_2 version of the a gene. Early in meiosis, the partner chromosomes physically pair, during which time single subunits from each chromosome in the pair (nonsister chromatids) can break and rejoin, essentially switching places with each other. The mechanics of this switch or crossover are such that the pieces of the two participating nonsister chromatids that are distal to the position of the crossover event with respect to the centromere end up being attached to the centromere of what was originally the partner chromosome (i.e., crossing over results in a reciprocal exchange of pieces of nonsister chromatids that are distal to the crossover event with respect to the centromere). Following pairing and crossing over, the partner chromosomes separate from each other (i.e., segregate at the first meiotic division) and proceed through the remainder of meiosis independently. The overall effect of crossing

[2] Throughout the remainder of this paper, the syllable *cross* will be replaced by the letter X when the terms crossover and crossing over are components of names of specific chromosome configurations (i.e., particular spatial arrangements of chromosomes at static points during meiosis).

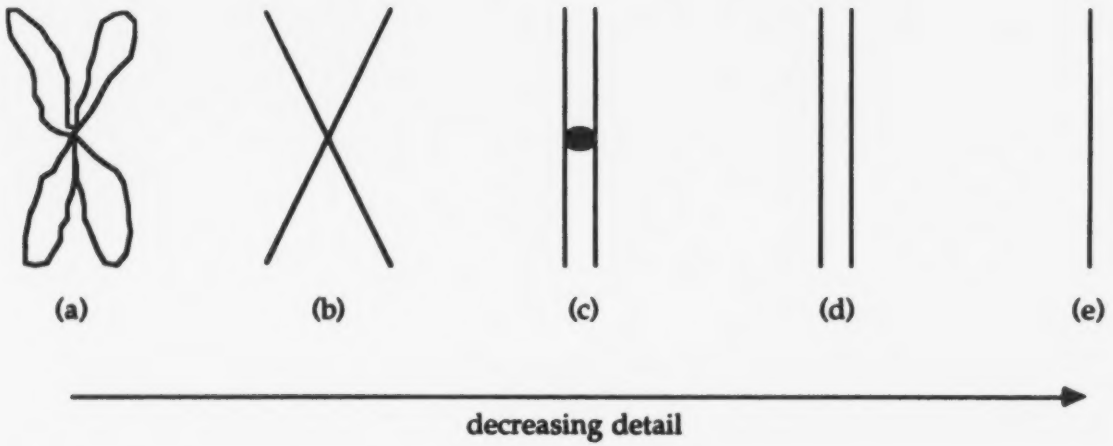


Figure 3. Replicated chromosome representations. (a) diagrammatic representation including dimensionality, shape, the presence of the centromere (implied by shape), and the presence of two sister chromatids, (b) X-shaped representation including shape, the presence of the centromere (implied by shape), and the presence of two sister chromatids, (c) parallel-line representation including the presence of the centromere (indicated by the dot) and the presence of two sister chromatids, (d) parallel-line representation including the presence of two sister chromatids, (e) single-line representation including none of the four structural features of replicated chromosomes.

over is to shuffle genes around between partner chromosomes, sometimes creating new combinations of different versions of different genes in each of the partners and ultimately in the sex cells produced as a result of meiosis. Highlights of the preceding description are illustrated in Figure 4. This figure not only illustrates the preceding verbal description, but also demonstrates the value of diagrams in clarifying spatial and structural relationships necessary for building some understanding of the process of interest. (For more details about the entire process, see Appendix A.)

Participants' Meiosis Knowledge

All 15 participants in this study spontaneously generated diagrams while working on the problem shown in Figure 1. These diagrams consisted of representations of chromosomes and of chromosome configurations (i.e., of particular spatial arrangements of chromosomes at static points during meiosis). Because solving the problem is essentially equivalent to exposing one's model of meiosis, participants' work, including their diagrams, was used to evaluate their models of chromosomes and of the process of meiosis.

Of the 15 participants, 2 experts and 3 experienced novices displayed completely correct chromosome/process models, 3 experts and 1 experienced novice displayed correct chromosome models and slightly flawed process models, and 1 experienced novice and all 5 inexperienced novices displayed flawed chromosome and process models. Specifically with regard to models of crossing over, 7 of the 9 participants who had correct chromosome models also displayed correct knowledge concerning the significance of particular chromosome structural features (i.e., the presence of two subunits and the position of the centromere with respect to genes of interest in the problem) to the outcome of crossing over. The 2 who did not spontaneously expose this knowledge did so upon further probing (to be described later). Among

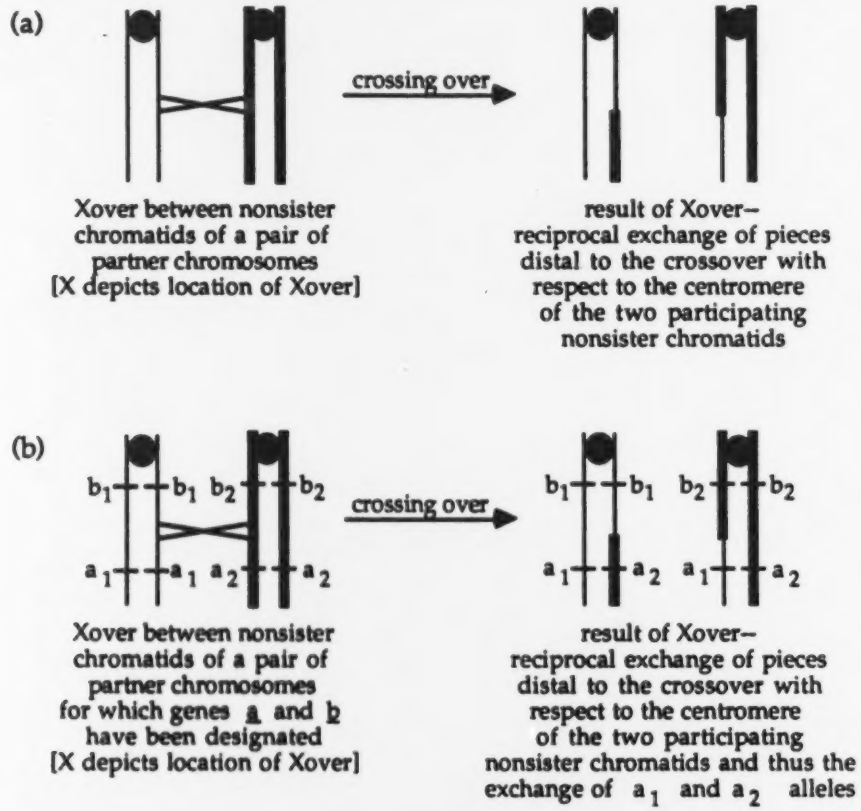

(a)
crossing over
Xover between nonsister chromatids of a pair of partner chromosomes [X depicts location of Xover]
result of Xover– reciprocal exchange of pieces distal to the crossover with respect to the centromere of the two participating nonsister chromatids
(b)
b1 b1 b2 b2
a1 a1 a2 a2
crossing over
b1 b1 b2 b2
a1 a2 a1 a2
Xover between nonsister chromatids of a pair of partner chromosomes for which genes a and b have been designated [X depicts location of Xover]
result of Xover– reciprocal exchange of pieces distal to the crossover with respect to the centromere of the two participating nonsister chromatids and thus the exchange of a1 and a2 alleles

Figure 4. Results of crossing over during meiosis. Individual lines represent chromatids and dots represent centromeres. Partner chromosomes are distinguished by the thickness of the lines representing sister chromatids. In (a) and (b), a Xover configuration appears on the left and a post-Xover configuration appears on the right. (a) illustrates the reciprocal recombination of pieces of nonsister chromatids and (b) highlights the effect of this recombination on particular allele arrangements. In (b), the crossover results in two of the four chromatids containing ab allele combinations that differ from the original chromosomes. In addition, (b) shows that given a cen-b-X-a relative order, a_1b_1/a_2b_1 and a_1b_2/a_2b_2 allele combinations will continue through the remainder of meiosis. Had the gene order been reversed as follows, cen-a-X-b, the allele combinations that would continue through meiosis are a_1b_1/a_1b_2 and a_2b_1/a_2b_2.

the 6 participants who displayed flawed chromosome and process models, only one harbored a process model in which the presence of two chromosomal subunits and the centromere affected the outcome of crossing over, and she did not recognize the significance of these two structural features (to be described later).

Throughout the remainder of this paper, I will refer to the 9 participants who displayed correct chromosome models and correct or nearly correct process models as *more expert* and to the 6 participants who displayed flawed chromosome and process models as *less expert*.

Knowledge-dependent Representational Variability

A key feature distinguishing the more expert participants from the less expert participants is the knowledge-dependent representational variability displayed by those in the more expert group. The two primary components of this feature are (1) the number of different chromosome representations used by an individual throughout his/her work (different according to the combination of the four chromosome structural features included in the representation) and (2) the nature and timing of differential feature inclusion. Results concerning the first of these two components are summarized in Figure 5. This figure illustrates that among the more expert participants, there was a greater tendency to generate and use a variety of representations of replicated chromosomes, including the use of allele letters alone without the explicit representation of the body of the chromosome. The less expert participants generated and used, at most, two different representations of entities having the same structure as replicated chromosomes.[3] (See Appendix B for computed-generated reproductions of participants' chromosome representations.)

[3] For most of the less expert participants, entities having the four structural features of replicated chromosomes were not replicated chromosomes according to their flawed chromosome models.

More Expert Participants' Representations of Replicated Chromosomes

# of subjects	# of different* representations
3	2
3	3
1	4
1	5
1	8

plus 4 of 9 sometimes used only allele letters

Less Expert Participants' Representations of Entities Having the Same Structure as Replicated Chromosomes

at most, two different* representations of same entity

Figure 5. Summary of representational variability associated with participant-generated chromosome representations. *Different here means different according to the chromosome structural features (dimensionality, shape, # of subunits (chromatids), centromere) included in the representation.

The second component, the nature and timing of differential feature inclusion, is summarized in Figure 6. This figure shows that the less expert participants often drew chromosome representations that more literally depicted chromosome appearance under a light microscope, typically including both dimensionality and shape, the two structural features that functionally have no bearing on the mechanics of meiosis.[4] At the opposite extreme, two of the less expert participants sometimes included little structural detail even when unrepresented structural features did have some bearing on the mechanics of meiosis. Further, the limited representational variability displayed by these participants tended to be associated with enhancing representations to more literally depict chromosome structure/appearance and not to be tied to any particular reasoning situation in a knowledge dependent way.

Figure 6 also shows that, in contrast to the less expert participants, the more expert participants tended to change their chromosome representations in response to task demands, including chromosome features that were biologically relevant to the immediate problem-solving situation. These changes typically occurred when crossing over was recognized as relevant to a problem solution: The two subunits of each chromosome (or at least the participating nonsister chromatids) and the centromere, the two structural features crucial to the mechanics of crossing over, were included by most of the more expert participants in chromosome configuration diagrams generated for dealing with crossing over (i.e., pairing and Xover configurations). Some members of the more expert group also removed unnecessary structural detail from subsequently drawn post-Xover configuration diagrams while maintaining needed information concerning the fate of particular alleles (versions of genes) following crossing over (i.e., information concerning

[4] The packaging of DNA molecules and associated proteins that give rise to dimensionality and shape does impact the molecular mechanism of crossing over. However, the molecular basis of crossing over is not of concern to this work.

Less Expert Participants

- tended to generate more literal depictions of chromosome appearance including features as follows:

• dimensionality	3/6 (only inexperienced novices)
• shape	5/6 (all inexperienced novices)
• subunit structure	5/6 single line or object/subunit (i.e. represented both subunits)
• centromere	1/6-no cen (mentioned or depicted)
	3/6-added cen when explaining chromosome structure or cen function in chromosome movement
	2/6-cen always included in more literal representations

- limited representational variability associated with enhancing representations to more literally depict chromosome structure/appearance and not tied to any particular reasoning situation
  - 4/6-same chromosome representation throughout problem solving
    - 2/4-switched to different chromosome representation during follow-up questioning
  - 2/6-one chromosome representation for problem solutions and different (more literal) chromosome representation in response to follow-up questions

(Figure 6 continued on next page)

More Expert Participants

- changed chromosome representations while problem solving in response to task demands
- tended to include chromosome features that were biologically relevant to immediate problem solving, for the most part not including dimensionality or shape
- changes occurred when crossing over was recognized as relevant to problem solution (correctly timed Xing over)

- in initial replicated chromosome representations
  - 1/9-alleles letters only (i.e. did not represent body of chromosome)
  - 5/9-single line
    (i.e., did not explicitly represent both chromosomal subunits)
  - 3/9-two lines (i.e., explicitly represented both chromosomal subunits)
  - 0/9-explicit representation of centromere

- in pairing and Xover configuration diagrams
  - 9/9-two lines (i.e., explicitly represented both chromosomal subunits)
    - 3/9-occasionally represented only nonsister chromatids of a pair of chromosomes
      (i.e., the subunits participating in crossing over)
  - 7/9-represented centromeres
  - 2/9-did not represent centromeres and also displayed flawed knowledge about the significance of cen position to Xing over

- in post-Xover configuration diagrams
  - 5/9-same features as in pairing & Xover configuration diagrams
  - 4/9-removed some structural detail but represented necessary segregation information

---

Figure 6. Nature and timing of differential feature inclusion in participant-generated chromosome representations.

allelic segregation at the first meiotic division). Interestingly, the 2 more expert participants who displayed some flawed knowledge about the significance of the position of the centromere to crossing over and who also did not include centromeres in relevant chromosome configuration diagrams corrected their flawed knowledge when viewing relevant chromosome configuration diagrams that contained the two subunit structure and/or centromeres. In addition to the fine-tuning of chromosome representations in response to crossing over and its consequences, none of the more expert participants ever represented chromosome dimensionality and only one ever represented chromosome shape,[5] the two structural features that have no bearing on meiosis. Finally, some examples of the more expert participants' fine-tuned changes are shown and fully explained in Figure 7.[6]

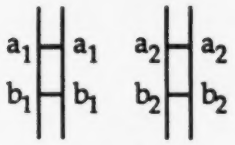
Systematic Uses of Fine-tuned Diagrams

As the more expert participants generated chromosome representations that were fine-tuned to the relevant biology, they used these representations in systematic ways in their problem solving. In general, the more expert participants used their fine-tuned diagrams to (1) support internal thought processes while formulating the solution to a problem (i.e., to support the computation or derivation of needed information), (2) record information (i.e., to keep track of computed or derived information for multi-step problem solving), (3) check preceding reasoning by repeating (1) and/or (2) using previously or newly generated diagrams, and (4) illustrate components of their problem solutions. The first three uses of diagrams differed from the fourth in that using diagrams to support thought

[5] The more expert participant who included shape in her chromosome representations used shape as a means for pictorially distinguishing between different chromosomes (i.e., chromosomes containing different genes).

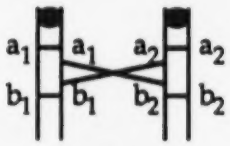
[6] Diagrams that occur in this and subsequent figures are computer-generated versions of individual participant's own spontaneously-generated diagrams.

Initial Representation

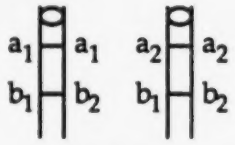


ab pairing configuration

Gamete Set (iii): Solution 1

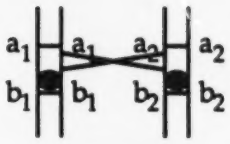


ab Xover configuration

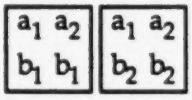


ab post-Xover configuration

Gamete Set (iii): Solution 4



ab Xover configuration



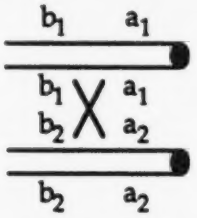
ab post-Xover configuration

Expert 2 explicitly depicted each chromosomal subunit in his initial chromosome representation. He then added centromeres to chromosome representations in Xover configuration diagrams. He later removed chromosome structural detail from his Solution 4 ab post-Xover configuration diagram while maintaining segregation information by enclosing appropriate sets of alleles in boxes.

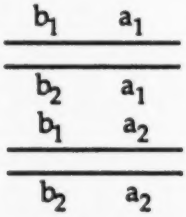
Initial Representation

replicated ab chromosome

Gamete Set (iii): Solution 1



ab Xover configuration

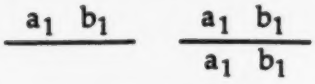


ab post-Xover configuration

Expert 4 did not explicitly depict the two chromosomal subunits in his initial chromosome representation. He then added two chromosomal subunits and centromeres to each chromosome representation in his ab Xover configuration diagram. He later removed centromeres from his ab post-Xover configuration diagram while maintaining segregation information by retaining the two-subunit structure in this diagram.

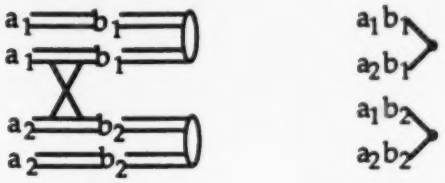
(Figure 7 continued on next page)

Initial Representation



replicated ab chromosomes

Gamete Set (iii): Solution 3



ab Xover configuration

ab post-Xover configuration

Gamete Set (iii): Solution 2

hybrid ab double-Xover/post-Xover configuration

ab post-Xover configuration

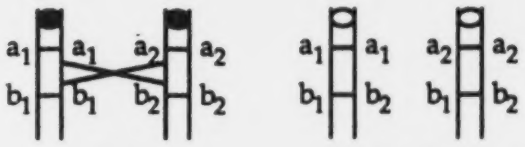
Expert 5 did not explicitly depict the two chromosomal subunits in her initial chromosome representations. She did however imply the existence of two subunits by associating two sets of alleles with the single line in one of her ab replicated chromosome representations. In her Solution 3 ab Xover configuration diagram, she not only explicitly added two subunits and centromeres to her replicated chromosome representations, but also used two lines to represent the double-stranded DNA molecule that makes up each subunit. In her Solution 3 ab post-Xover configuration diagram, she removed much of this structural detail while maintaining segregation information by showing sets of alleles attached to centromeres. In her Solution 2 hybrid ab double-Xover/post-Xover configuration diagram, expert 5 drew only the participating nonsister chromatids, arranging post-Xover alleles as she worked through the two Xovers. In her Solution 2 ab post-Xover configuration diagram, she included allele letters for all four subunits but no structural detail. She did, however, maintain segregation information through the order in which allele pairs appear, that is, a_1b_1 and a_2b_1 segregate together and a_1b_2 and a_2b_2 segregate together.

Figure 7. Examples of more expert fine-tuned diagram changes.

processes during solution formulation, to record information, and to check preceding reasoning were participant-centered activities occurring when individuals were actively engaged in some aspect of problem solving, whereas using diagrams to illustrate was an other-centered activity occurring after some verbal indication that problem solving was complete. However, all four general diagram uses share the feature that some piece or pieces of an individual's meiosis model was externalized in a form that made salient the spatial relationships among the represented entities and among the depicted structural features of those entities. Because of the focus on reasoning in this study, I will elaborate on the first three systematic diagram uses in the remainder of this paper.

Figure 8 contains specific examples of diagrams used by some of the participants for computation, derivation, and record keeping for multi-step problem solving. Comparison of Figure 8 (a-c) and (d-e) illustrates the distinction between computation (8/a-c) and derivation (8/d-e). Computation (in the algorithmic sense) involves producing and using a diagram of one chromosome configuration to determine the specific form of a subsequently occurring chromosome configuration much like one might write out two large numbers, one above the other, and use them to compute their product. In other words, some new information that does not exist in the original diagram is computed from it. The common example shown in Figure 8 (a) is to draw and utilize an ab Xover configuration to compute the corresponding ab post-Xover configuration. Derivation entails extracting information inherent in a diagram that is needed to continue or complete problem solving much like one might inspect a graph to derive information about its underlying function. In other words, information already existing in the diagram is derived from it. This diagram use was less common than computation, one example being the derivation of centromere position from an ab post-Xover configuration diagram as shown in Figure 8 (d). Finally, Figure 8 (e/upper) also

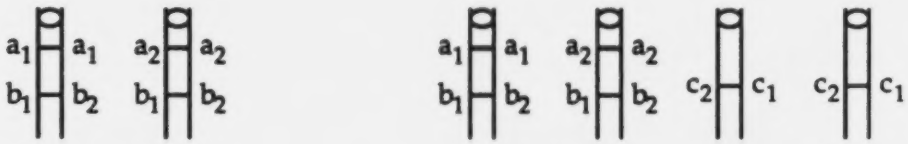
(a)



ab Xover configuration | ab post-Xover configuration

use diagram of pairing or Xover configuration to compute post-Xover configuration (e.g., physically trace through the Xover by placing pencil at left cen and trace from cen to a_1 across to b_2 to compute ab post-Xover allele combinations)

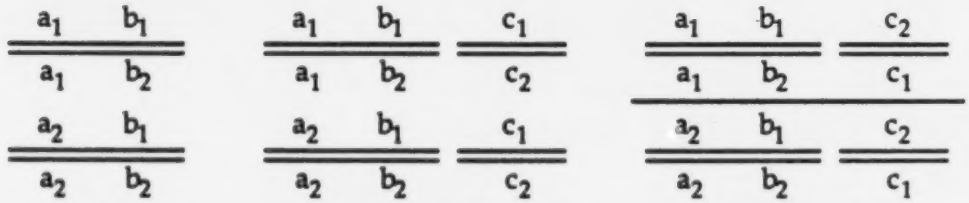
(b)



ab post-Xover configuration | ab post-Xover configuration | c post-Xover configuration

use diagram of post-Xover configuration to compute behavior of remaining chromosome pair (e.g., given the depicted ab post-Xover configuration and the gamete set [$a_1b_1c_2$ $a_1b_2c_1$ $a_2b_1c_2$ $a_2b_2c_1$], the need for a c chromosome Xover between the c gene and the centromere can be computed from the a_1b_1/a_1b_2 allele combination on the left ab post-Xover chromosome)

(c)



ab post-Xover configuration | alignment I configuration | alignment II configuration

use diagram of alignment I configuration to compute alignment II (post-segregation I) configuration (e.g., given the depicted ab post-Xover configuration and the gamete set [$a_1b_1c_2$ $a_1b_2c_1$ $a_2b_1c_2$ $a_2b_2c_1$], the depicted alignment II configuration can be computed from the a_1b_1/a_1b_2 allele combination on the upper ab post-Xover chromosome)

(Figure 8 continued on next page)

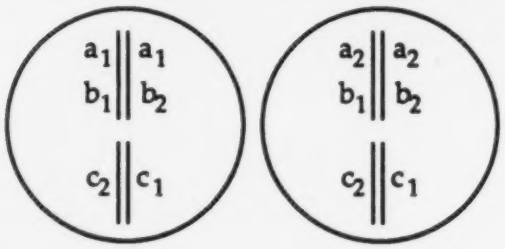
(d)

$a_1\ b_1$	$\circ\!\!-\!\!-\ a_1\ b_1$
$a_1\ b_2$	$\circ\!\!-\!\!-\ a_1\ b_2$
$a_2\ b_1$	$\circ\!\!-\!\!-\ a_2\ b_1$
$a_2\ b_2$	$\circ\!\!-\!\!-\ a_2\ b_2$
ab gamete combinations	ab post-Xover configuration

use diagram of post-Xover or alignment I configuration to derive cen position (e.g., assuming that the ab gamete combinations as written represent the post-Xover or alignment I ab chromatid pairings, that is, a_1b_1/a_1b_2 are attached to the same centromere and a_2b_1/a_2b_2 are attached to the same centromere following crossing over between genes a and b, the centromere position can be derived from the fact that b alleles have switched places as a result of crossing over and the a alleles have not)

(e)

$\circ\!\!-\!\!-\ b_1\ a_1$	$\circ\!\!-\!\!-\ b_1\ a_1\ \ c_2$
$\circ\!\!-\!\!-\ b_1\ a_2$	$\circ\!\!-\!\!-\ b_1\ a_2\ \ c_2$
$\circ\!\!-\!\!-\ b_2\ a_1$	$\circ\!\!-\!\!-\ b_2\ a_1\ \ c_1$
$\circ\!\!-\!\!-\ b_2\ a_2$	$\circ\!\!-\!\!-\ b_2\ a_2\ \ c_1$
ab post-Xover configuration	alignment I configuration



post-segregation I configuration

a_1	a_1	a_2	a_2
b_1	b_2	b_1	b_2
c_2	c_1	c_2	c_1

gamete genotypes

use diagram of alignment I or post-segregation I configuration to derive c chromosome behavior relative to ab chromosome behavior (e.g., the need for c chromosome crossing over can be derived from the arrangement of c alleles in alignment I or post-segregation I configurations constructed from gamete genotypes)

Figure 8. Examples of more expert systematic diagram uses.

illustrates the record-keeping use of diagrams in multi-step problem solving. Here, a participant drew the ab post-Xover configuration as the result of a preceding computation or derivation (the record), then changed the diagram by adding c alleles to appropriate ab allele combinations (according to the given gamete information), then derived information concerning the occurrence of crossing over between the c chromosome pair from the alignment I configuration diagram.

Generalized observable behaviors were considered indicative of particular diagram uses. Specific patterns of behavior associated with computation, derivation, record keeping in multi-step problem solving, and checking are summarized in Figure 9. Patterns for the first three activities consisted of three similar steps: (1) drawing a relevant chromosome configuration, (2) pausing to look at or touch the diagram generated in step (1), and (3) describing/drawing the next solution component. For checking, notable behaviors included (1) referring back to previously constructed diagrams (records) and repeating relevant observable problem-solving behaviors listed above at the completion of a problem and (2) explicitly stating the intention to check some component of a solution followed by drawing and repeating relevant observable problem-solving behaviors listed above.

Less Expert Diagram Use Related to Crossing Over

I noted earlier that among the less expert participants, only one exposed a model of meiosis in which the presence of two chromosomal subunits and the centromere affected the outcome of crossing over. While she routinely included these two chromosome structural features, along with dimensionality and shape, in her chromosome representations and drew chromosome configurations similar to those of the more expert participants when dealing with crossing over, she apparently did not know or recognize the significance of the two subunits and

Use	Observable behaviors
COMPUTATION	• draw relevant chromosome configuration • trace through (Xover) OR look at diagram (PAUSE) • describe/draw computed chromosome configuration
DERIVATION	• draw relevant chromosome configuration • look at diagram (PAUSE) • describe/draw derived chromosome configuration
RECORD KEEPING IN MULTI-STEP SOLUTION	• draw result of some computation (e.g., an ab Xover configuration) • look at (PAUSE for computation or derivation) • complete next step of problem solving
CHECKING	• refer back to previously constructed diagrams and repeat observable problem-solving behaviors • "let's check" followed by drawing

Figure 9. Observable behaviors associated with the systematic diagram uses exhibited by more expert participants.

centromere to crossing over or utilize her diagrams in the same way as more expert individuals. Her drawings of an ab Xover and its corresponding ab post-Xover configurations are shown in Figure 10. According to the mechanics of crossing over, the gene/Xover/centromere arrangement in her ab Xover configuration diagram should result in the reciprocal exchange of an a_1 and an a_2 allele (because the a gene is distal to the crossover with respect to the centromere). However, her ab post-Xover configuration diagram, generated without any overt reference to her ab Xover configuration diagram, indicates that two b alleles rather than two a alleles have been exchanged. When asked later if switching the order of the a and b genes from ab to ba would affect the outcome of crossing over, this less expert participant replied, "No, it wouldn't make any difference. It's arbitrary." This response indicates both that she was unaware of the significance of gene order with respect to the centromere to crossing over and that even a well specified diagram (i.e., one containing all necessary features) cannot support accurate reasoning in the absence of relevant pieces of knowledge.

Discussion

Role Played by Diagrams in More Expert Reasoning

Having defined and characterized specific systematic diagram uses common to more expert individuals and absent among less expert individuals, I now turn to the more general cognitive role played by diagrams in more expert reasoning about process. The systematic diagram uses displayed by experts shared a similar observable pattern--drawing, followed by pausing to look at/touch the diagram, followed by describing/drawing the next solution component. The initial diagram in this cycle is an externalized version of relevant pieces of a problem solver's meiosis model that makes salient the spatial relationships among the represented entities and among the depicted structural features of those entities. I propose that

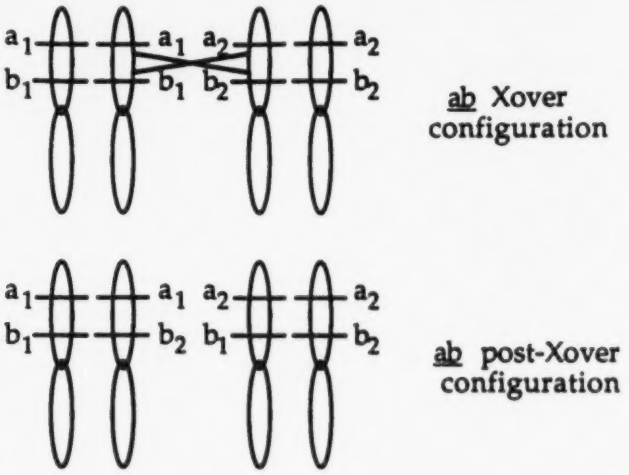


Figure 10. Less expert participant's ab Xover and ab post-Xover configuration diagrams.

the initial diagram in the cycle generally serves as an external storage device that frees working memory, allowing for the performance of additional cognitive tasks, and that these cognitive tasks are being performed during the pause when the problem solver is looking at or touching the diagram. Specifically, when computing from a diagram, the problem solver is visualizing or running through relevant chromosome movements/interactions, possibly mentally manipulating diagram components; when deriving information, he/she is evaluating information inherent in the diagram; when record keeping, he/she is storing information with potential later relevance; and when checking, he/she is assessing the accuracy of previous reasoning by verifying previous computations and derivations.

This interpretation is supported by spontaneous comments made by some of the more expert participants as they worked on the meiosis-reasoning problem. Three of the more expert participants used motion-oriented language in relation to specific diagrams as follows (drawing behaviors are explained parenthetically in boldface type):

> As I was thinking, I sent those together **[points to one set of ab and c chromosomes in the post-segregation I configuration]**. And then I'm gonna turn that over **[points to one c post-Xover chromosome in the post-segregation I configuration]** and send c_2 with a_1 and b_1 through the second division so we can get those gametes **[referring to the third gamete set]**.

> ... the idea is to put all the chromosomes there **[adds a_1b_1 sister chromatid to ab Xover configuration]**. So if I had a_1a_1 here and b_1b_1 there **[points to upper chromatids in ab Xover configuration]** and I had a crossover here **[traces X in ab Xover configuration]**, that puts a_2 on that **[points to cen dot on upper chromatid and draws arrow up from centromere]** centromere which I just put on top, so I put it on top **[points to upper post-Xover configuration]**. And it puts a_1 on this **[points cen dot on lower chromatid]** centromere which I moved down **[draws arrow down from lower centromere]**. Whereas b_1 stays on that **[points to b_1 and motions above ab Xover configuration]** and b_2 stays on that **[points to b_2 and motions below ab Xover configuration]**.

> If you have a crossover here **[adds X to diagram]** then that will put a_2 up here and a_1 down here, **[adds a alleles to diagram]** and if you have another crossover **[adds X to diagram]** it will put b_1 up here and b_2 down there. **[adds b alleles to diagram]** And that'll generate the same ones that you had before. **[glance at Solution 3 post-Xover ab chromosomes]** **[10 sec pause-writing out ab post-Xover configuration]** And that'll do it.

Others made the following comments about their reasons for drawing.

> ... I have to look, I have to work it out and see. I haven't thought about this in a long time and it's not obvious, it's not intuitive by looking at it. I have to draw it out and see ....
>
> I can't visualize it without writing it out.
>
> So, just drawing it out to see how the recombination event occurs.
>
> Well, this is the first one I'm gonna have to work with. I'm gonna have to write [draw] to figure this one out, because I don't think my brain can retain much more than that this time.
>
> ... drawing pictures ... is like a record keeping that enables me to be more nearly sure that I'm right. I can go back and check and trace things when I have drawings.

Based on the kind of language used when discussing diagrammatic reasoning and comments about drawing while problem solving, more expert individuals do seem to think in terms of manipulating diagram components and to at some level perceive the value of and reasons for using diagrams while reasoning.

Coevolution of Meiosis Knowledge and Pictorial Skill

Given the kinds of results presented above, it is clear that an intricate interconnection exists between meiosis knowledge and pictorial skill. Among more expert individuals, when specific meiosis knowledge is present and recognized as relevant to the immediate reasoning task, fine-tuned diagrams including this knowledge are routinely generated and used for the completion of the task. In addition, diagrams in which relevant knowledge is represented can cue recognition of the relevance of that knowledge to the immediate reasoning situation. In contrast, less expert individuals tend to either overspecify their diagrams by representing what they know best regardless of its relevance to problem solving, that is chromosome appearance including dimensionality and shape, or underspecify their diagrams by leaving out components relevant to the immediate reasoning task. Further, unlike the cuing provided by a well specified diagram in the context of a more expert knowledge base, a well specified diagram alone cannot make up for pieces of knowledge missing from a less expert knowledge base.

This interconnection between meiosis knowledge and pictorial skill and the differences in the quality and uses of diagrams exhibited by more versus less expert individuals are suggestive of an important aspect of developing understanding of meiosis; namely, that meiosis knowledge and pictorial skill coevolve. Coevolution here means that meiosis knowledge and pictorial skill mutually influence one another in the development of understanding where a meaningful understanding of meiosis includes specific knowledge about the process and participating entities and knowledge about domain-specific diagrams. In one direction of influence, the development of understanding includes gains in knowledge about how to efficiently represent different aspects of meiosis knowledge and about the utility of using diagrams in particular reasoning situations. In the other direction of influence, pictorial representations support the construction of an accurate mental model of the process. These proposals are elaborated below.

With regard to the first direction of influence, it is possible that pictorial skill increases as understanding increases because of a need to juggle the many pieces of knowledge inherent in a more developed knowledge base when reasoning about meiosis. The intricately interconnected nature of the process of meiosis dictates that a problem-solving task requiring reasoning about the process involves the activation of many components of a more expert knowledge base. As was noted earlier, in all of the drawing behaviors exhibited by the more expert participants, fine-tuned diagrams served as information storage devices that freed working memory for the performance of additional cognitive activities for problem solving. The more expert participants in essence used fine-tuned diagrams as "tools to think with". Interestingly, many aspects of the more expert participants' pictorial reasoning behaviors corroborate the theoretical analyses of diagram use in problem solving advanced by Larkin and Simon (1987) and Larkin (1989). In these analyses, the primary role of diagrams in problem solving is to reduce the load on working

memory by serving as information storage devices, a role plainly demonstrated in this study. Further, diagrams were proposed to facilitate problem solving by grouping information according to location and supporting perceptual inferences through the display of features and relationships essential to problem solving, and by cuing related information not initially represented. Diagrams generated by the more expert participants in this study obviously grouped and made salient the features and spatial relationships important for reasoning about meiosis. Likewise, they apparently supported making perceptual inferences like visualizing particular chromosome movements as well as cuing additional relevant information.

With regard to the second direction of influence, the more expert participants' reasoning behaviors and their own comments about visualizing aspects of meiosis through the use of diagrams suggest that diagrams might play a role in building knowledge about meiosis. Well-constructed diagrams clearly make important spatial and structural relationships among chromosomes and their component parts visible. By relying on human's highly developed system of visual perception to see and encode these relationships and how they change as a result of the action of particular meiotic events, diagrams may facilitate (1) the addition of pieces of meiosis knowledge to an individual's knowledge base and (2) the breaking of inappropriate connections and establishment of appropriate connections between pieces of knowledge in an individual's knowledge base. This facilitation would, of course, require an understanding of the representational elements in a diagram or diagrams. Further, it would require additional guidance concerning, for example, the constraints imposed by certain structural features as was evidenced by one of the less expert participant's lack of recognition of the significance of the centromere in crossing over even in the face of a well-specified diagram.

Educational Implications

Specific results of this study and the derived proposals concerning the coevolution of meiosis knowledge and pictorial skill suggest a need for some fundamental changes to standard meiosis instruction. Although diagrams are ubiquitous in meiosis instruction, the pictorial skills and reasoning exhibited by the more expert participants in this study are virtually never addressed. If diagrams serve as more than illustrative devices in a more expert knowledge base and if meiosis knowledge and pictorial skill do in fact coevolve, then instruction concerning more expert pictorial skills and reasoning must be incorporated into meiosis instruction in order to support the development of a meaningful understanding of this process.

Toward this end, I offer some general instructional changes that could be relatively easily incorporated into meiosis instruction. First, carefully design instructional diagrams and include explanations that address (a) meanings of various representational objects, (b) reasons for representing certain features in particular diagrams, and (c) relationships among different representations of the same entity and/or event in different diagrams (also suggested by Cho et al., 1985; Thomson & Stewart, 1985). Second, explicitly treat diagrams as expressions of knowledge and as learning/reasoning tools rather than simply as illustrative devices by (a) interweaving verbal and pictorial descriptions of meiosis and (b) encouraging students generally and through specifically designed tasks to draw diagrams of verbally presented information and vice versa (small-scale implementation by Thomsom & Stewart, 1985). Third, provide students with meiosis reasoning situations (like the research problem used here; also see Kinnear, 1989 and Kinnear & Martin, 1989 for another example) and include instruction about, modelling of, and practice with diagram-dependent reasoning. Finally, assess

both verbal and pictorial knowledge/reasoning. I intend to design and test meiosis instruction based on these suggestions.

While this work has focused on the process of meiosis for reasons stated earlier, it seems a reasonable assumption that understanding and reasoning about meiosis is substantially similar to understanding and reasoning about other subcellular biological processes as well as other natural processes that involve nonarbitrary interactions between microscopic and submicroscopic entities. If so, the results of this work not only have implications for meiosis instruction, but are also applicable to instruction in a wide variety of subjects and domains like biochemistry, cellular physiology, and organic chemistry. In addition to these more general educational implications, this work provides empirical support for proposals concerning the role played by diagrams in problem solving and scientific reasoning as well as a novel empirical view of the nature of reasoning about essentially invisible natural processes.

References

Cho, H.-H., Kahle, J. B., & Nordland, F. H. (1985). An investigation of high school textbooks as a source of misconceptions and difficulties in genetics and some suggestions for teaching genetics. *Science Education, 69*(5), 707-719.

Hackling, M. W., & Lawrence, J. A. (1988). Expert and novice solutions of genetic pedigree problems. *Journal of Research in Science Teaching, 25*(7), 531-546.

Hildebrand, A. C. (1985). *Conceptual problems associated with understanding genetics: A review of the literature on genetics learning*. University of California, Berkeley.

Hildebrand, A. C. (1989). *Pictorial representations and understanding genetics: An expert/novice study of meiosis knowledge*. University of California, Berkeley (UMI order number 9103719).

Kindfield, A. C. H. (in press). Confusing chromosome number and structure: A common student error. *Journal of Biological Education*.

Kinnear, J. (1989). *Kangasaurus*. Danbury, CT: EME.

Kinnear, J., & Martin, M. (1989, March). *Problem solving in a computer-based setting with verbal to visual recoding of given data*. Paper presented at the annual meeting of the National Association for Research in Science Teaching, San Francisco.

Larkin, J. H. (1989). Display-based problem solving. In D. Klahr, & K. Kotovsky (Ed.), *Complex information processing: The impact of Herbert A. Simon* (pp. 319-341). Hillsdale, NJ: Lawrence Erlbaum.

Larkin, J. H., & Simon, H. A. (1987). Why a diagram is (sometimes) worth ten thousand words. *Cognitive Science, 11*, 65-99.

Slack, S. J., & Stewart, J. (1990). High school students' problem-solving performance on realistic genetics problems. *Journal of Research in Science Teaching, 27*(1), 55-67.

Smith, M. U. (1988). Successful and unsuccessful problem solving in classical genetics pedigrees. *Journal of Research in Science Teaching, 25*(6), 411-433.

Smith, M. U. (1990, April). *Cell division: Student misconceptions and instructional implications*. Paper presented at the Annual Meeting of the National Association for Research in Science Teaching, Atlanta.

Stewart, J., & Dale, M. (1989). High school students' understanding of chromosome/gene behavior during meiosis. *Science Education, 73*(4), 501-522.

Stewart, J., Hafner, B., & Dale, M. (1990). Students' alternate views of meiosis. *American Biology Teacher, 52*(4), 228-232.

Thomson, N., & Stewart, J. (1985). Secondary school genetics instruction: making problem solving explicit and meaningful. *Journal of Biological Education, 19* (1), 53-62.

Appendix A

Meiosis Review

Meiosis-related concepts described in the following subsections are illustrated in accompanying Figure 11 at the end of this appendix.

Ploidy

Turning first to chromosome number, each species of organism has a characteristic number of different chromosomes. Each different chromosome contains a subset of all the genes that are characteristic of that species. One set of all the different chromosomes constitutes the genetic make-up of that species. A cell nucleus that contains one set of all the different chromosomes for that species is said to be haploid or to contain the haploid number (N) of chromosomes. A cell nucleus that contains two sets of all the different chromosomes for that species is said to be diploid or to contain the diploid number (2N) of chromosomes. In essence, a diploid cell contains two 'copies' of each of the different chromosomes characteristic for that organism. In a diploid cell, the two 'copies' of a given chromosome are said to be homologous to one another and constitute a homologous pair of chromosomes. The two chromosomes of a homologous pair are 'copies' in the sense that they contain that same genes and the genes contained in each of those chromosomes are positioned at the same location along the length of each chromosome. Homologous chromosomes also have similar physical structures at the beginning of meiosis. However, they are not necessarily identical copies of one another in the sense that the specific genetic information present for each of the genes (i.e., the specific alleles) along the length of each chromosome can vary.

Chromosome Structure

Before replication, each chromosome consists of a single double-helical DNA molecule containing single copies of all the unique genes[7] that make up that chromosome. When a chromosome replicates, the result is a chromosome consisting of two identical double-helical DNA molecules called 'sister chromatids' that are physically attached to one another at a point called the 'centromere'.[8] The consequence of this is that a replicated chromosome now contains two identical copies of each of the unique genes that make up that chromosome. Both unreplicated and replicated chromosomes are referred to simply as 'chromosomes'. When replication occurs, the number of chromosomes (discrete physical entities) present in the cell remains the same while the amount of DNA and the number of genes is doubled. Technically, the term 'chromatid' only refers to each of the subunits of a replicated chromosome. Calling an unreplicated chromosome a chromatid is an inaccurate/inappropriate use of the term 'chromatid'.

The process of replication occurs once at a specific time during the cell cycle[9] preceding mitosis or meiosis and cell division.[10] Prior to replication, all chromosomes in a cell nucleus are unreplicated. Following replication, thus at the beginning of meiosis, all chromosomes in a cell nucleus are replicated. Following

---

[7] Unique genes are genes that occur once in the haploid genetic constitution of an organism. The genes a, b, and c are unique genes for the hypothetical organism in the meiosis problem in Figure 1.

[8] The DNA of both unreplicated and replicated chromosomes is associated with a variety of proteins, but the presence and functions of these proteins have no significant bearing on solving the meiosis problem in Figure 1.

[9] 'cell cycle' refers to the growth cycle of a cell which includes five successive phases, G1--S-G2-M-C. The process of replication occurs during S phase and either mitosis or meiosis (both nuclear divisions) occurs during M phase just prior to cytokinesis or cell division that occurs during C phase. Thus, the processes of replication and meiosis are temporally separated by the G2 phase of the cell cycle. Although other processes that contribute to nuclear and cell division occur during G2, these processes are irrelevant to solving the meiosis problem in Figure 1, and therefore are not considered in this review of meiosis knowledge.

[10] Technically, mitosis and meiosis are nuclear divisions that may or may not be followed by cell division depending on particular species characteristics and cell type characteristics within particular species.

nuclear division, the resulting nuclei now contain unreplicated chromosomes until they reach the point in their individual cell cycles that DNA/chromosome replication occurs again. It is only during mitosis or meiosis, and thus after chromosomes are replicated, that they are condensed into forms that are visible as discrete entities under a light microscope.

Process Aspects of Meiosis

Two related components comprise the process aspects of meiosis: stages (meiosis I and meiosis II) and phases (prophase I, metaphase I, anaphase I, telophase I, prophase II, metaphase II, anaphase II, and telophase II (where Is and IIs refer to stages)).

Stages. In the first stage of meiosis, a single diploid nucleus divides into two nuclei (intermediate products of meiosis). During the second stage of meiosis, each of the nuclei produced as a result of meiosis I divides again resulting in the formation of a total of four haploid nuclei (final products of meiosis), two from each of the products of meiosis I.

Phases. The process of meiosis consists of a series of systematic chromosome movements/interactions that ultimately result in the production of four haploid nuclei from a single diploid nucleus. Subprocesses or events characterized by particular spatial arrangements of chromosomes and/or specific chromosome movements/interactions define the phases of the overall continuous process. The correspondence between the phases of meiosis and the events of importance is as follows: *prophase I*-homologous pairing and recombination or crossing over,[11] *metaphase I*-alignment of homologous pairs of chromosomes (alignment I), *anaphase I*-segregation of homologues to separate nuclei (segregation I) [transition

[11] For the purposes of this presentation, I will continue to use only the term 'crossing over' to refer to this meiotic event.

from meiosis I to meiosis II], *metaphase II*-alignment of individual 'replicated'[12] chromosomes (alignment II), and *anaphase II*-segregation of sister chromatids to separate nuclei (segregation II). Although the phase names (prophase, metaphase, etc.) have historical and cytological importance, they are not particularly descriptive of the subprocesses they represent. For this reason, in the remainder of this paper, I use the more descriptive labels for the events that appear in parentheses rather than the conventional phase names. While acknowledging that replication is not a part of the process of meiosis, I will subsequently group it with the six meiotic events because it is a necessary prerequisite of meiosis.[13] Of the seven total events, six of them--replication, homologous pairing, alignment I, segregation I, alignment II, segregation II--necessarily occur when a cell nucleus undergoes meiosis. The seventh, crossing over, is not necessary for the completion of meiosis and its occurrence or lack thereof has a significant effect on the outcome of a single meiosis. Of particular importance are the relative positions of the centromere, gene(s) and crossover event(s).

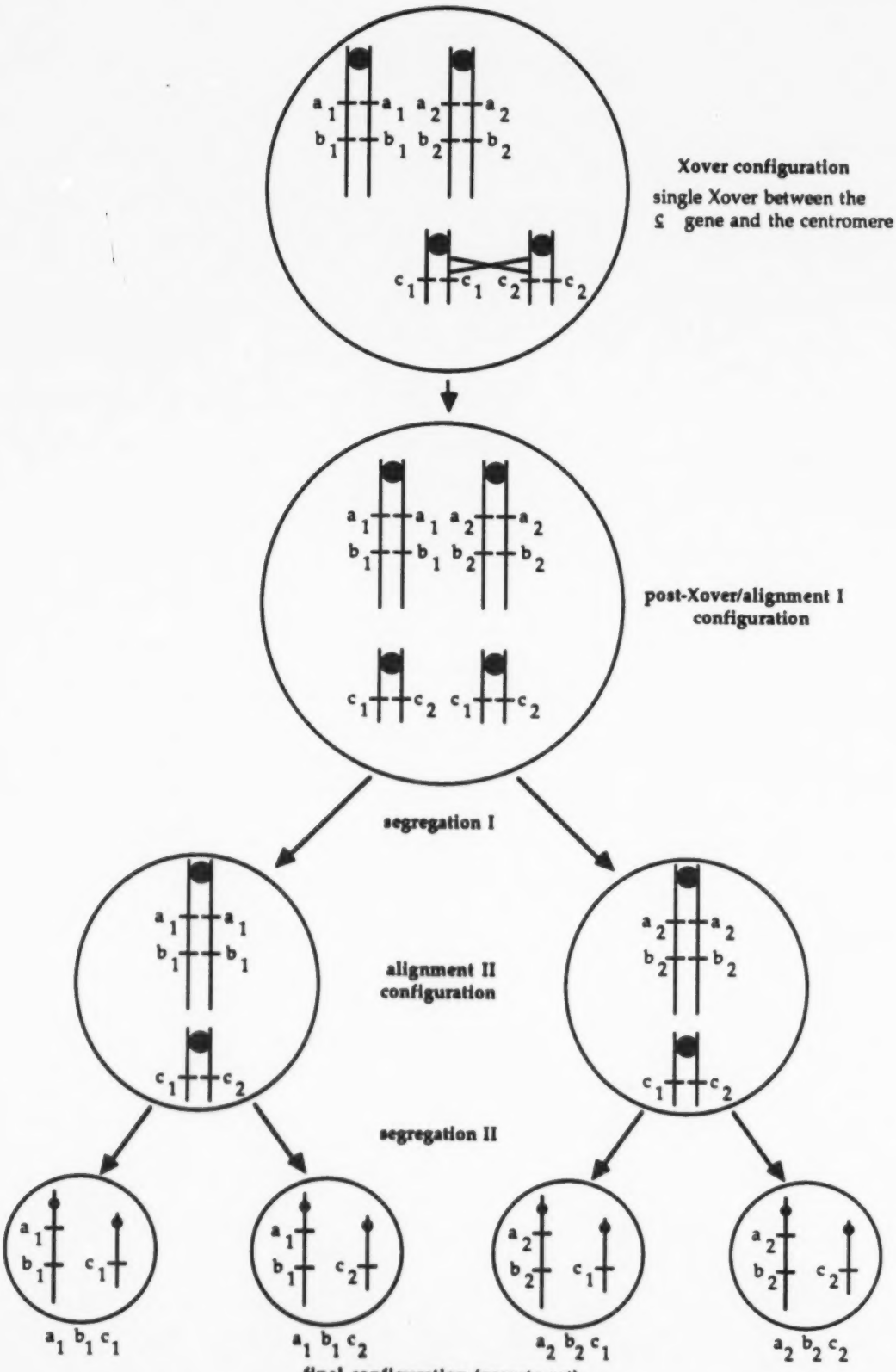
---

[12] The term 'replicated' is used here to refer to entities having the structure of replicated chromosomes. At this point in meiosis, however, sister chromatids of these entities may or may not be identical to one another depending on the previous occurrence of crossing over and the specific genetic constitution of the cell/organism in question.

[13] A not uncommon meiosis misconception is that DNA replication is actually part of the meiotic process.

Figure 11. Illustration of some important aspects of meiosis. The meiosis shown here is one possible solution to gamete set (ii) (see Figure 1). Configuration refers to particular spatial arrangements of chromosomes at static points during meiosis. In the Xover (i.e., crossover) configuration, chromosomes are replicated (lines=chromatids and dots=centromeres), homologous chromosomes (i.e., chromosomes containing the same genes (e.g., a and b) though possibly different alleles (e.g., a_1 vs a_2) of those genes) are paired, and the X between the two c chromosomes indicates the position of the crossover event. In the post-Xover/alignment I configuration, homologous pairs are aligned and the effect of the crossover event is reflected by the exchanged c_1 and c_2 alleles in the c chromosome pair. In the alignment II configuration, individual chromosomes that separated as a result of segregation I are aligned in the center of each intermediate nucleus. In the final configuration, each final product nucleus contains one of each unreplicated chromosome as a result of segregation II. According to the more classical view of ploidy, the initial nucleus is diploid (2N), that is, it contains two sets of ab and c chromosomes. The final nuclei are haploid (N), that is, each contains one set of ab and c chromosomes. Ploidy is essentially undefined for the transient intermediate nuclei. (See Kindfield, in press, for a discussion of the classical vs modern view of how ploidy changes throughout the cell cycle.)

(Figure 11 continued on next page)

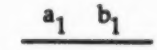

Xover configuration
single Xover between the
ς gene and the centromere
post-Xover/alignment I
configuration
segregation I
alignment II
configuration
segregation II
final configuration (gamete set)

Appendix B

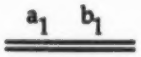
Participants' Chromosome Representations

More Expert Participants

Expert 1

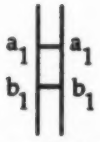


(a) replicated chromosome



(b) replicated chromosome

Expert 2



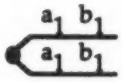
(a) replicated chromosome

(b) replicated chromosome

Expert 3

(a) unreplicated chromosome

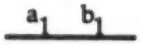
(b) replicated chromosome



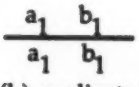
(c) replicated chromosome

(d) pre-Xover nonsister chromatids

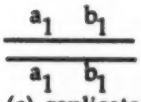
Expert 4



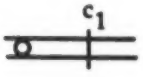
(a) replicated chromosome



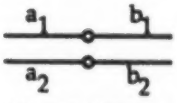
(b) replicated chromosome



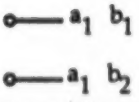
(c) replicated chromosome



(d) replicated chromosome

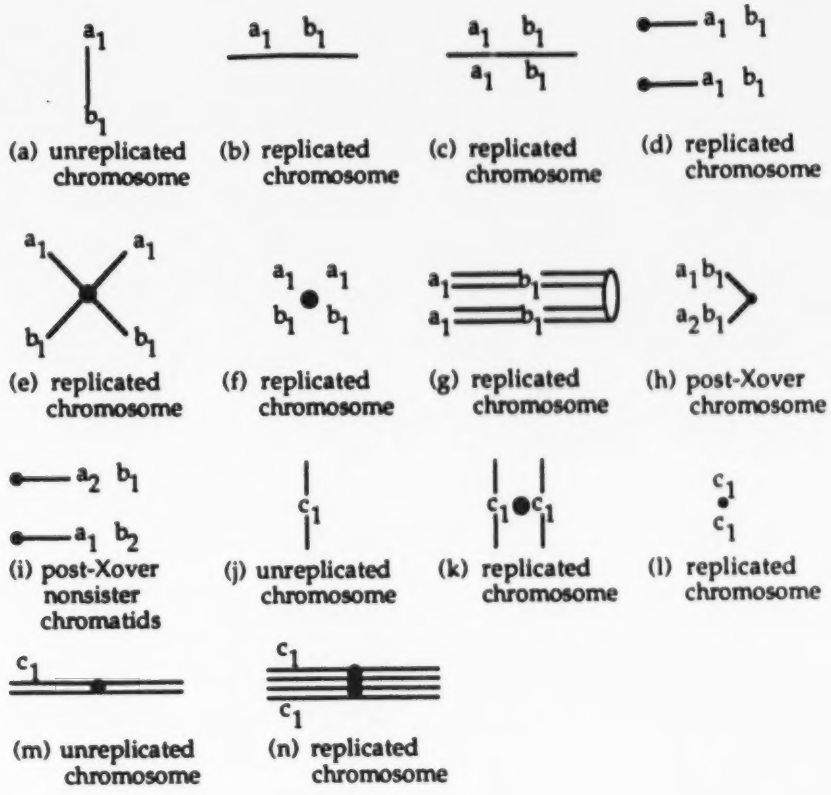


(e) pre-Xover nonsister chromatids

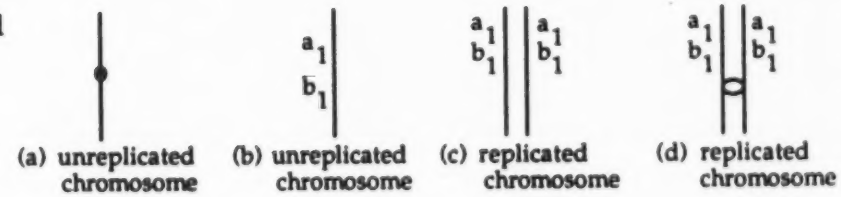


(f) post-Xover sister chromatids

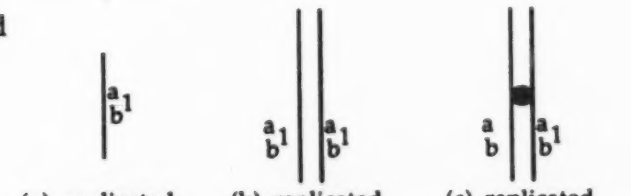
Expert 5



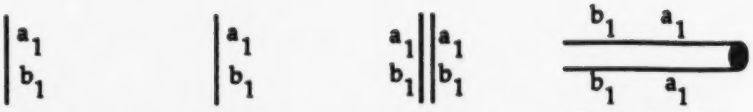
Experienced Novice 1



Experienced Novice 2



Experienced Novice 3



(a) unreplicated chromosome (b) replicated chromosome (c) replicated chromosome (d) replicated chromosome

Experienced Novice 4

(a) unreplicated chromosome (b) unreplicated ab chromosome (c) unreplicated ab chromosome (d) unreplicated c chromosome

(e) replicated ab chromosome (f) replicated ab chromosome (g) replicated c chromosome (h) replicated c chromosome

Less Expert Participants

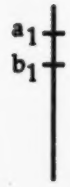
Experienced Novice 5

(a) unreplicated chromosome (b) replicated chromosome

(c) chromosome found in intermediate cells (d) chromosome found in intermediate cells

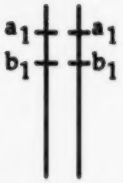
Inexperienced Novice 1

(a) unreplicated chromosome

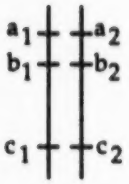


(b) unreplicated chromosome

(c) replicated chromosome

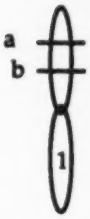


(d) replicated chromosome



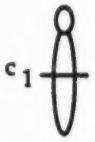
(e) pre-Xover nonsister chromatids

Inexperienced Novice 2

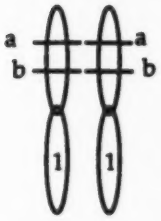


(a) unreplicated chromosome

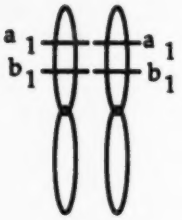
(b) unreplicated chromosome



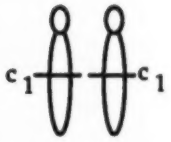
(c) unreplicated ς chromosom



(d) replicated chromosome

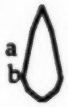


(e) replicated chromosome



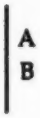
(f) replicated ς chromosom

Inexperienced
Novice 3



(a) unreplicated chromosome

(b) unreplicated chromosome



(c) unreplicated chromosome

(d) replicated chromosome

(e) replicated chromosome

Inexperienced
Novice 4

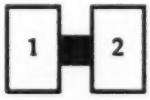
(a) chromatid OR haploid chromosome

(b) ab chromatid OR haploid ab chromosome

(c) ς chromatid OR haploid ς chromosome

(d) diploid chromosome in initial cell

(e) diploid ab chromosome in initial cell



(f) diploid ς chromosome in initial cell

Inexperienced
Novice 5

(a) unreplicated chromosome

(b) unreplicated chromosome

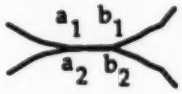
(c) replicated chromosome

(d) unreplicated ς chromosome

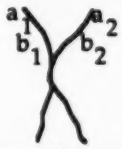
(e) replicated ς chromosome

(f) chromosome found in haploid cells

(g) unreplicated chromosome in initial cell



(h) unreplicated chromosome in initial cell



(i) unreplicated chromosome in initial cell